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THE HISTORY OF
PROTOZOOLOGY

ELERY R. BECKER

Department of Zoology

IOWA STATE COLLEGE

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THE HISTORY OF PROTOZOOLOGY



ANTONI VAN LEEUWENHOEK.

LID VAN DE KONINGHLYKE SOCIETEIT IN LONDON.

Obituaire van Deets. N. 1632.

Dit is de eerste keer dat een Nederlander is geweest in de Academie der Wetenschappen te Amsterdam. Hij is geboren te Leeuwarden den 24sten October 1632. Hij is overleden te Amsterdam den 26sten Augustus 1723. Hij heeft veel geleefd en veel geleerd. Hij heeft veel geleefd en veel geleerd. Hij heeft veel geleefd en veel geleerd.

ANTONI VAN LEEUWENHOEK (1632-1723)

From a mezzotint by J. Verkolje, 1686

[Frontispiece]

THE HISTORY OF PROTOZOOLOGY

TWO LECTURES DELIVERED BEFORE
THE UNIVERSITY OF LONDON AT
KING'S COLLEGE IN MAY 1925

BY

F. J. COLE, D.Sc. OXON

PROFESSOR OF ZOOLOGY, UNIVERSITY COLLEGE, READING

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PREFATORY NOTE

THESE lectures are based on material for a general history of Zoological Discovery which I have been collecting for many years, but only a small proportion of the material relating to the Protozoa could be utilised in the lectures. The further the work on this general history proceeds, the more obvious it becomes that the co-operation of specialists in the various groups is essential if approximate accuracy is to be maintained. As it happens, however, one cannot always count on finding the specialist who has an intimate and first-hand knowledge of the history of his group. In the field of Protozoology Bütschli is a conspicuous example of this rare combination, and his historical introductions are specially valuable because they are based on a personal and detailed examination of the original authorities. My friend, Mr. Clifford Dobell, F.R.S., may claim to share this distinction with Bütschli, and I owe him grateful acknowledgments for the very generous assistance he has been ready at all times to give me. Perhaps he will himself one day write the complete story of the history of Protozoology, of which the present work can only claim to be an outline.

The publication of these lectures has been aided by a grant from the Publication Fund of the University of London.

F. J. C.

24/5
May 12, 1925.

LECTURES ON THE HISTORY OF PROTOZOOLOGY

LECTURE I

THOSE of us who study the history of science soon learn to digest one unpalatable but wholesome truth, viz. that the mistakes we are called upon to chronicle, and occasionally to condemn, are only equalled by the mistakes on the part of the historian himself. When we first read the writings of the old naturalists we experience a feeling of disappointment, if not of contempt. Their statements appear to be indefinite and incoherent, as if they had no real conception of the phenomena with which they were grappling. They work painfully round a point without seeming, or even endeavouring, to approach it, until we begin to doubt whether they have anything tangible to communicate in language which we can understand. Now it is impossible to believe that this partial or apparent failure is due to any serious defect in their mental equipment, and hence we must fall back on the assumption that the fault lies in ourselves. It is true that the Latin of some of the older authors is a language almost of their own invention, and even those making use of the mother-tongue may be only less trying to interpret. As an instructive example of these minor difficulties I may mention that a passage in Malpighi was translated by one historian—"I saw with mine eyes a certain great

thing.” Another commentator corrected it to “I saw with mine eyes a great certain thing”—meaning that there was no doubt about it. They were both mistaken, for a contemporary French version makes it clear that what Malpighi *meant* to say was, “I saw with mine eyes a truly great thing.”

The real explanation of our doubts and misunderstandings is a failure to realise that what we have been taught to regard as immutable principles and facts are nothing but the fluid products of evolution which may fluctuate from year to year. Indeed, the further we trace them back the more they change, so that the problems which confronted the older workers have an aspect which is difficult for us to reproduce. Our scientific beliefs have reached their present form by passing through numerous preparatory stages. They are the cumulative results of a succession of researches which traverse every avenue of error and mystification, and only occasionally illustrate the truth. No discovery is ever made by one observer, but is built up with exceeding slowness and much futile labour until in the end it emerges, it may be quite suddenly and unexpectedly, to enjoy a more or less fleeting existence. This was recognised even in the seventeenth century. In 1685, according to Blumenbach, Drelincourt brought together as many as 262¹ “groundless hypotheses” concerning generation, which he proceeds to criticise with that degree of acerbity with which biologists are familiar. Nevertheless, “nothing is more certain than that his own theory formed the 263rd.”

Now how does this affect our attitude towards the old masters? We cannot hope to understand

¹ I do not understand how Blumenbach arrives at this figure, but I have seen only the 1686 edition,

them and to appreciate them at their true value until we are convinced that the principles and phenomena with which they are dealing are not those with which we are familiar. What they take for granted as facts we should describe by some other name, just as the guiding principles of to-day may possibly provoke the jests of the future biologist. Their vagueness is not due to unintelligence, but to the fact that they were working in an atmosphere which was less clarified than ours. We must therefore be prepared to dispossess ourselves of our modern bias before we undertake a journey in the company of these venerable guides. I admit that this is difficult, for we have to steer a course between the right-hand extreme of attributing to them a knowledge and subtlety they did not possess, and the left-hand extreme of denying that they played any essential part in the development of science. In illustration of this point let us take a simple example. Suppose we wished to discover the inventor of the binomial nomenclature. If we define the expression in the terms of the strict modern systematist, then its history is a very brief one—indeed, it is quite a modern creation. We cannot, however, ignore the fact that the modern systematist only made use of, and modified, the system in vogue before his time, and hence we must work backwards through many periods until we reach the *Systema* of Linnæus. But Linnæus himself only carried one step further a method of classification already in existence, and he cannot therefore be regarded as the end of our quest. The next stage of this bibliographic investigation is represented by the *Essay towards a Real Character and a Philosophical Language*, published by Dean Wilkins in 1668.

Now did Wilkins invent the binomial terminology? We find examples of it in his book—indeed, a number of binomials in use at the present moment appear there for the first time. But many of them are not defined, and perhaps none of his definitions, when given, would be accepted by a modern systematist. Also in some cases he uses an entire Latin sentence to define an animal instead of a binomial term, and it would be idle to claim that he had a conception of genus and species which would satisfy a modern systematist. Again, he is himself in this matter the direct successor of the sixteenth-century naturalists, such as Rondelet, who in their turn derived their inspiration from Aristotle. Admitting all this, however, we must still concede that the germ of the idea was in his mind, and that he foreshadowed that long series of developments which intervene between the involved Latin sentence of the sixteenth century and the clearly defined term of two words with which the contemporary biologist is familiar. Judged by modern standards Wilkins is negligible, but if we judge him according to the standard of the systematists of his own time, his work must be regarded as a deviation from the practice of his predecessors which made possible, centuries after his death, our own solution of the problem.

If we select from the literature of Protozoology those publications to which by general consent some importance can be assigned, and plot them out on squared paper so that we can form an impression of the growth of the subject as a whole,¹ we are struck with the fact that Protozoology is essentially

¹ I have already made use of this method in a statistical review of the History of Comparative Anatomy.

a modern study, and that before the year 1825 it had only received the casual attention of a handful of distinguished observers. This lack of continuous effort, and the absence of a relevant background, makes the earlier history of Protozoology difficult to weave into a coherent narrative. In modern times a noteworthy discovery meets with an immediate and energetic response, and we are therefore surprised that the description of *Vorticella* in 1677, of *Paramecium* in 1703, of *Amœba* in 1755, and the publication of the important monograph on the Infusoria by O. F. Müller in 1786, should have been received in comparative silence. There are, however, many reasons for this. The animals in question are minute, and hence, according to the genius of the time, unimportant and even contemptible. Man was not intended, they were told, to contemplate midges. Moreover, the difficulties of the work were formidable. An observer had often to grind his own lenses and make his own microscopes. It was not until 1824 that the first achromatic objectives were produced in England, and the principles on which our modern high-power lenses are constructed go no further back than the calculations of J. J. Lister of 1830. It is therefore to be expected that the work of the earlier observers would not be sufficiently accurate and detailed to disclose the unique claim which the Protozoa had on the attention of biologists. Ehrenberg's elaborate researches of 1838 not only failed to do this, but were actually misleading, since his object was to show that the Protozoa possessed a structure comparable with that of the higher animals, and in consequence their distinctive interest was for the time being completely obscured. The

improvements in the microscope, however, soon produced their effect. The cell theory was launched in 1838-9, and the inauguration of the histological method with all the accompanying refinements of microscopical research followed as a logical necessity. In 1845 von Siebold reduced contemporary knowledge to a common formula, and, by establishing for the time the unicellular conception of the Protozoa, provided an expanding stimulus to research which has survived to our own time.¹

The Nummulitic limestones which extend across Europe and Northern Africa into India in a broad band, in places several thousand feet thick, were known to the ancients, and therefore they were in a sense acquainted with the fossil Protozoa. Examples of the complex species *Nummulites gizehensis* are mentioned by the geographer Strabo, who refers to the tradition that they are petrifications of the lentils left behind by the builders of the Pyramids.

The first reference to the Protozoa in print, according to d'Archiac and Haime, is by the botanist Clusius (c. 1550), who mentions that during the retreat of the Tartars before the Teuton soldiers coins were freely scattered as they fled with the object of diverting the pursuit. This manœuvre might have been successful, had the coins not been turned into stones (i.e. *Nummulites*) by the intervention of an obliging and sympathetic Deity.

Gesner's account of the Foraminiferan *Vaginulina*, published in 1565, is the earliest record of a Protozoan as an animal. He regarded it, however, as a small mollusc belonging to the genus *Strombus*. The

¹ Siebold's views can no longer be maintained. Mr. Dobell's non-cellular conception of the Protozoa is much nearer the truth.

first illustration of a Protozoan is to be found in the *Micrographia* of Robert Hooke issued in 1665, the species in question being probably *Rotalia beccarii*. He says: "I was trying several small and single Magnifying Glasses, and casually viewing a parcel of white sand, when I perceiv'd one of the grains exactly shap'd and wreath'd like a Shell, but endeavouring to distinguish it with my naked eye, it was so very small, that I was fain again to make use of the Glass to find it; then, whilst I thus look'd on it, with a Pin I separated all the rest of the granules of Sand, and found it afterwards to appear to the naked eye an exceeding small white spot, no bigger than the point of a Pin. Afterwards I view'd it every way with a better *Microscope*, and found it on both sides, and edge-ways, to resemble the Shell of a small Water-Snail with a flat spiral shell."

Of all the older naturalists perhaps the most familiar figure is that of the Dutch microscopist, Leeuwenhoek. Much sympathy, traceable to the delightful but not altogether accurate sketch of Leeuwenhoek published in 1885 by Benjamin Ward Richardson, has been wasted on this wonderful old man. He was not merely a parish beadle deputed to open and shut the door of the council chamber, and show honour and respect to the councillors of the little town of Delft, but a respected tradesman in easy circumstances who had sufficient if not ample leisure to devote to scientific pursuits. Most of his results were communicated to our own Royal Society in the form of letters, of which about 130 more or less abridged extracts were published in the *Philosophical Transactions*, counting the 5 in Hooke's *Philosophical Collections*. His last published letter

was written in 1723 in his 91st year. In a previous letter, dated 1720, he says that he is $88\frac{1}{4}$ years old and "in the autumn of his life."

That Leeuwenhoek must be regarded as the father of Protozoology is beyond question. This will be evident even from the very brief consideration of his discoveries which I am able to give. In a letter dated 1676 and published in 1677 he describes for the first time, but without figures, a free living Protozoan—a species of *Vorticella*, which he first saw in standing rain-water in 1675. Later, in 1703, he figures both *Vorticella* and *Carchesium*. "These little animals," he says, "are the most wretched creatures I have ever seen," but his reasons for this unfavourable opinion are not very convincing. The peristomial cilia are interpreted as "two little horns which were continually moved after the fashion of a horse's ears"—an error of observation which will be readily understood. He describes the stalk and its manner of contraction, but later on when he returned to the subject he gives a better account of this part of the animal. Other Ciliates are described in the same letter, one of which was probably *Stylonychia*.

In 1677 Leeuwenhoek was the first to observe cilia, and he also recognised their use. He mentions them repeatedly in his writings. The revolving motion of *Volvox* he attributes to the action of cilia. Of the Rotifers he found in pepper infusions he says in 1687: "In this way they occasioned such a circular eddy in the water that not only several small bodies floating in the water were moved in a circular manner, but even many very minute animalculæ, though able to swim vigorously, when they approached the larger animalculæ were

whirled about for some time in a circular manner" (Sharpey).

For the first account of a parasitic Protozoan we are also indebted to Leeuwenhoek. In 1681 he found in his own fæces a parasite of which he published a description in 1682. This is the earliest record of the occurrence of intestinal Protozoa in man. The species in question was the Flagellate *Lamblia* (*Giardia*) *intestinalis* and not *Balantidium coli* as usually stated. Later, in 1683, Leeuwenhoek finds *Opalina* in the fæces of the frog, and possibly *Nyctotherus*. "In the month of June," he says, "I met with some frogs whose excrement was full of an innumerable company of living creatures, of different sorts and sizes. . . . The whole excrement was so full of living things that it seemed all to move."

An important discovery, described and figured by Leeuwenhoek in 1700, was that of *Volvox*, which he found in ditch water. He comments on their movement and rotation. He saw that each sphere consisted of a multitude of particles, and noted small spheres inside the large ones. He watched all the small spheres escape from the large ones, recognised that they grew rapidly after liberation, and thus prepared themselves for independent existence.

The well-known Foraminiferan *Polystomella* was described and figured by Leeuwenhoek in 1702 in a letter dated June 2, 1700. "I was desirous," he says, "of knowing what was the food of the shrimp, and I had observed that the part in these creatures which we call the head was not only the head but the belly of the shrimp whence I concluded that there its stomach might be found. In some of the shrimps' stomachs I found some exceeding minute shells,

which, on account of their round figure, I called Snails, and which were not larger than a large grain of sand, and to show the pretty shape of these shells, I thought it would not be amiss to give a drawing of one of them as viewed through the microscope" (Hoole).

Passing over an early published description and figure of an Infusorian—*Colpoda*—by Buonanni in 1691, the next important contribution to the literature of Protozoology was by Harris, who discovered *Euglena viridis* in 1696. He says: "I look't on a small Drop of the Green Surface of some Puddle-water which stood in my Yard, this I found to be altogether composed of Animals of several Shapes and Magnitudes; But the most remarkable were those which I found gave the Water that Green Colour, and were Oval Creatures, whose middle part was of a Grass Green, but each end Clear and Transparent. They would contract and dilate themselves, tumble over and over many times together, and then shoot away like Fishes: Their Head was at their broadest end, for they still moved that way. They were very Numerous, but yet so large, that I could distinguish them very plainly with a Glass that did not magnify very much."

In 1703 an important communication by an anonymous writer, whose identity has not been penetrated, appeared in No. 284 of the *Philosophical Transactions*, following a letter by Leeuwenhoek in No. 283. He worked with infusions of pepper, and used simple and compound microscopes which he claims could give him a magnification equal to 640 diameters, but his method of arriving at this figure is very crude. He mentions that some people have questioned the truth of Leeuwenhoek's

descriptions, but that "as far as he was able to follow him he had always found him faithful in matters of fact." In this paper, besides observations on various Bacteria and *Euplotes*, we have the first description and figure of *Paramecium*, and the first figure, after Leeuwenhoek, of *Vorticella*. He describes the contraction of the stalk in *Vorticella* and the contraction and expansion of the "fringed or bearded Mouth." He states that "a rapid stream runs constantly toward their fore part, as if they drew in water, but I rather believe this current is made by a nimble tremulous motion of some minute Fins or Legs, which my Glasses will not discover." He describes the ciliation and habits of *Paramecium*, the cilia being referred to as "very minute feet," and he notes that they are not of uniform length. Some of his "feet" were possibly trichocysts. He also observed transverse fission in the Infusoria, which, however, was wrongly interpreted as an act of sexual union. Fission was further studied by Trembley in 1745.

The first separate treatise devoted to the Protozoa was the work of Joblot on the Infusoria published in 1718. He was the first to describe the contractile vacuole. His views on spontaneous generation will be dealt with later.

In 1753 Baker published the first description of *Noctiluca* and its phosphorescent properties, based on a letter he had received from one Sparshall. The first figure of *Noctiluca* is that by Slabber, bearing the date of 1778. Sparshall describes the pelagic habit of the genus, and says that it resembles "an exceeding minute Worm . . . hanging with its Tail fixed to an opaque Spot in a kind of Bladder."

He attributes the "sparkling of sea water" to this animal.

One of the most remarkable and beautiful works of natural history is the *Monthly Insect Diversions* of Roesel of Nürnberg, the first number of which appeared in 1741. This work is usually bound up in four dated volumes, but the dates of the individual parts are unfortunately unknown. Roesel was by profession a miniature painter and engraver, and his scientific work was accomplished with microscopes which he had made himself, and it was illustrated by magnificent plates drawn and engraved by his own hands. To him we owe first and foremost the discovery of *Amæba*, which he described and figured in 1755. To him also we owe the first account of the structure and movement of living matter or protoplasm. He calls *Amæba* "the small Proteus," under the impression that it was a smaller species of the Proteus of Baker, which, however, is a Ciliate. He figures it natural size and enlarged. He says he was puzzled to know what its proper shape was, and whether it had a head and a tail, but that these matters became clear to him by observing continuously the behaviour of a single individual. He thus became familiar with its changing shape and pseudopodia, its division by fission, and the stiffer ectoplasm and more fluid granular endoplasm. He saw all this, he adds, not once but several times. He observed also apparently a case in which the stiffer ectoplasm had ruptured allowing the endoplasm to escape. Had he not missed the nucleus and contractile vacuole his description would have been wonderfully complete. The discovery of *Amæba*, however, is by no means Roesel's only contribution to Protozoology.

ology. He describes and figures the structure and life-history of *Volvox*, and gives us excellent illustrated accounts of various Vorticellids and *Stentor*. His figures were much the best that had up to his time been published.

Ledermüller is said by Bütschli to have introduced that popular term Infusoria in 1763. He does make use of the expression "Infusion animals," but the Latin equivalent Infusoria was probably first employed by Wrisberg in 1765.

Ehrenberg and Oscar Schmidt are often stated to be the discoverers of the trichocysts of Ciliata, but these structures were first demonstrated in *Paramecium* in 1770 by John Ellis, better known for his work on the animal nature of Zoophytes, who calls the trichocysts the "fins" of the animal. His account is particularly interesting as an early example of the employment of experimental methods. The juice of the geranium, he finds, causes the *Paramecium* to become torpid, contract, and finally to discharge the trichocysts, which then appear "like so many bristles all round their bodies." The length of the trichocyst is estimated as half the diameter of the middle of the body. When transferred to fresh water the Paramecia expand and resume their movements, the "fins" becoming again invisible.

In 1773 O. F. Müller discovers the Dinoflagellata, and in 1776 he describes, but does not figure until 1786, the common species of *Ceratium* as *Cercaria tripos*, under the impression that it was related to the Distomid larva of that name. His important monograph on the Infusoria was published posthumously in 1786, and was the first general work on the Infusoria which had any pretensions to complete-

ness. His Infusoria, however, included, besides the Protozoa, Bacteria, Diatoms, Vinegar Worms, Planarian Worms, Cercaria larvæ, Rotifers and other odds and ends of animals, provided that they were sufficiently small. His classification in fact was based on external characters only, and although he recognised the distinction between those animals which possessed an internal structure, such as the Rotifers, and the Infusoria *sensu stricto*, in which there were no traces of organisation, he hesitated to embody this knowledge in his classification, with the result that he included in the same group a Bacillus and a Vinegar Worm. The consequence was to plunge the classification of the Protozoa into greater confusion than ever. Müller regarded the Infusoria as the simplest of all animals, and described 378 species in his monograph, of which about 150 are valid. He transferred *Stentor* from the Polypes to the Vorticellidæ, and described and figured conjugation in *Paramecium*—a phenomenon, however, which had previously been known to Leeuwenhoek.

The beautiful and well-known genus *Actinosphærium* was first described and figured by Eichhorn in 1783. In 1812 a striking physiological observation was made by Gruithuisen, who was the first to describe the circulation of the endoplasm in *Paramecium*. This important advance, the full significance of which was unfortunately not realised by Ehrenberg and his contemporaries, was confirmed by C. G. Carus in 1834, Dujardin in 1835, Focke in 1836, and Erdl in 1841. A similar phenomenon had long previously, in 1774, been described in the plant cell by Corti.

The term Protozoa was first used by Goldfuss in

1817, but not definitely introduced until 1820. It was first employed in the modern sense by von Siebold in 1845. Goldfuss included in the group, however, the Polypes and Medusæ.

In 1826 d'Orbigny, then only twenty-three years of age, instituted the Foraminifera, and was the first to make a systematic study of the group. Of this work Parker and Jones in 1871 remark that "with all its faults, and they are neither few nor small, the *Tableau Méthodique* of d'Orbigny must be regarded as the alphabet of the nomenclature of the Foraminifera." He was the first to draw attention to the extraordinary diverse and complex nature of many Foraminiferan shells. *Globigerina* is one of the forms here described for the first time. Misled, however, by the superficial resemblance of some of them to the shells of Mollusca, especially *Nautilus* and *Spirula*, he attributes a high degree of organisation to the Foraminifera, and considers them to be "microscopic Cephalopoda." This startling "discovery" was, in fact, conceived by his father, and inherited and developed by d'Orbigny himself. It was, of course, the purest assumption, as neither father nor son had adequately investigated the living animal with a reliable microscope. This, however, did not prevent d'Orbigny describing the living Foraminiferan in the following terms: "The Cephalopoda of this Order have a bursiform body, in the posterior portion of which the shell is enclosed; this body is sometimes of great volume compared with that of the head, to which it serves as a refuge in moments of danger, enclosing it almost entirely in the anterior folds of the skin. This head is very small, slightly, or not at all, distinct from the body, and terminated by numerous ten-

tacles, which are disposed in several rows round the mouth, which is central.”¹ The humble but elevating pleasures of the imagination, which we are so often told are incompatible with the scientific temperament, are nevertheless here seen in full flight in the speculations of a French naturalist.

Dufour in 1826 gives us the first detailed account of one of the Sporozoa, which he afterwards, in 1828, named *Gregarina*. It was found in the alimentary canal of several species of Coleoptera, and subsequently in the gut of the earwig. He regards them as minute Entozoa belonging probably to the Trematoda. He observed the well-known triple division of the gregarine body, but interprets it as either a case of sexual union or of spontaneous fission. Siebold, who investigated the genus in 1837 and 1839, at first denied that it was a completely formed animal, and asserted that it was the egg of an insect. This view, however, he withdrew, and finally classified the parasite with the Cystic Entozoa. He gives an excellent description of that interesting form of association known as syzygy. Schleiden, Henle and others recognised the unicellular structure of *Gregarina*, but regarded it as an overgrown plant cell, and it was not until 1848 that Kölliker demonstrated the Protozoan affinities of the genus.

In 1828 commence the important and numerous publications of Ehrenberg on the Protozoa, and in 1838 he published his large work on the Infusoria, in which 350 species are described from his own observations. His Infusoria include the Protozoa, Bacteria, Diatoms, Desmids, and Rotifers, all of which he regards as animals, but he rejects Cercaria,

¹ Quoted from Heron-Allen.

Spermatozoon, and Anguillula. The description of the Rotifers constitutes about one-third of his large work. He institutes a new group called the Phytozoa, which consists of two classes, (1) the Polygastrica, with many stomachs, and (2) the Rotatoria, with a single stomach. The Polygastrica include the Mastigophora, Rhizopoda, Ciliata, Acinetaria, Bacteria, Diatoms, and Desmids—in fact, all those organisms in which a complex gut was suggested by indigo feeding, and all were supposed to be organised in the same way as the larger animals, i.e. they were complete and perfect. Hence the title of his beautiful monograph—"The Infusion Animals as *complete* Organisms."

The idea of a complex type of organisation in the Protozoa was not new. Von Baer in 1827 had expressed the view that even the lowest organisms must have an internal nutritive surface distinct from the external circumscribing one, but he hesitated to apply this doctrine to the whole of the Protozoa. Ehrenberg was led to adopt the theory as the result of his feeding experiments. Von Gleichen in 1778 had already fed Infusoria with Carmine, and had correctly described the formation of the food vacuoles and the discharge of the undigested residue. Ehrenberg repeats these experiments over a period of ten years, but his conclusions are different. He finds it necessary to use absolutely pure colours free from the lead which was a common adulterant at the time, and the colours he prefers are Carmine, Sap Green, and Indigo—especially the last. He notes the rapid passage of the pigment into the "stomachs" in the interior of the body, and its final extrusion, and concludes that the polygastric organisms may have a com-

plex gut consisting of mouth, œsophagus, as many as 200 stomachs, spiral intestine, anus, and a possible pancreas. There is no absorption of food by the external surface of the body. In all cases the colouring matter passes into the interior of the animal. The gut may be simple in structure, but is always present. Further, the body as a whole is often divided into a head and trunk. In addition to the gut there may be a complex muscular system, of which the "contractile" thread in the stalk of *Vorticella*, which he discovered, is an example. He interprets the contractile vacuole as the seminal vesicle, the nucleus as the testis, and the granules of the endoplasm as eggs which are discharged by the anus. He is undecided as to whether nervous and vascular systems are definitely present. In 1839 the polygastric theory was criticised by Meyen in the following passage: "Many observers have already questioned these assertions of M. Ehrenberg; for my own part I never admitted them, because, in the first place, I never could see the intestines which form the communication between the stomachs, and likewise because I have observed, many years since, that these supposed stomachs were moving in the interior of the body of many species with great rapidity, in the same manner as the granules which circulate in the joints of *Chara*." Ehrenberg's fundamental error, therefore, was in not observing that the so-called stomachs moved independently of each other within the endoplasm, and therefore could not be connected up with a definite gut, and his assumption that they were part of a visceral system is one of the strangest and most unfortunate mistakes ever made by a highly competent observer. He himself, however,

consistently refused to admit his errors, and replied to his critics by publishing very detailed illustrations of the organisation of the Polygastrica, but, as von Siebold truly remarked, "detailed as they may be, they are not representations of nature." Huxley also in 1851 observes that Ehrenberg's researches were "wonderful monuments of intense and unremitting labour, but at least as wonderful illustrations of what zoological and physiological reasoning should *not* be."

As Ehrenberg professed to have discovered the polygastric structure in a Monad it is obvious that he must have had at his disposal microscopes of tolerable efficiency. One of his pupils states that he possessed a microscope which magnified 2,000 diameters. This is doubtless a mistake, but he certainly used a French microscope made by Chevalier of Paris, which gave him a magnification of 800 diameters, although he generally worked at from 300-400 diameters. His objects were measured with a glass micrometer scale made by Dollond of London, on which half a line ($\frac{1}{24}$ of an inch) was divided into 400 equal parts. With the additional assistance of a micrometer screw made in Berlin he claimed that he could measure down to $\frac{1}{48000}$ of an inch.

Ehrenberg ignored evolution and the cell theory, but he opposed spontaneous generation on the ground that he had discovered genitalia in the Infusoria, the absence of which had been held to support the view that their only avenue to existence was by spontaneous synthesis. He instituted a large number of now well-known genera, such as *Euglena*, *Carchesium*, *Actinophrys*, *Bodo*, *Arcella*, *Acineta* and *Dendrosoma*, he recognised the affinities

of the naked and testaceous Lobosa, but described early stages of *Aurelia* as parasitic Infusoria.

If Ehrenberg's polygastric hypothesis can be said to have enjoyed an independent existence at all, it certainly did not long survive the period of its birth. It is necessary to add, however, that a belief in the complexity of the Protozoa in a modified form was maintained by many observers after Ehrenberg, and, as Sharp and others have recently shown, may still be true! Ehrenberg's classification naturally shared the fate of the polygastric theory, and the Bacteria, Diatoms, Desmids, and Rotifers were speedily ejected from the Infusoria by his immediate successors. Ehrenberg, in fact, was not only behind his time, but lacked the mental equipment which can discern and establish general principles. Had this not been so, and had he been able to appreciate the philosophical bearings of the problems which lay before him, a man of his great observational powers and industry could have placed the study of Protozoology on an unassailable foundation. It was, however, by one of his contemporaries that this task was accomplished.

Dujardin published his first important communication on the Protozoa in 1835, and in 1841 he issued the general treatise on the Infusoria which represents his final pronouncement on these animals. He is the first observer to bring a powerful and original mind to bear on the structural problems of a considerable body of Protozoa, but we must not forget that his early work coincided with great improvements in the compound microscope. He was the first to make a careful study of *living* Foraminifera. From his observations on *Gromia* and other genera he soon convinced himself that

the shell was not internal, as d'Orbigny believed, but external; and also that there were no complex respiratory organs or molluscan tentacles. He studied the soft parts by crushing the shell or decalcifying it, and showed that the Foraminifera were not Mollusca, nor did they fall within any established group of the animal kingdom. He studied the structure and streaming movements of the substance of which they were formed, which he found to be the same in all species investigated, and named it *Sarcode*. He successfully challenges the polygastric theory of Ehrenberg, without, however, absolutely excluding the possibility of fibres and organs being present in the Sarcode; and also demonstrated the falsity of the Cephalopod interpretation of the Foraminifera to d'Orbigny himself—again, however, with a reservation that *some* of d'Orbigny's species might be Molluscs. The constitution of the Foraminifera was thus a simple one, and exhibited no traces of the complexity assumed by Ehrenberg and d'Orbigny. No evidence of a complex organisation was found even in that curious and interesting genus *Polytrema*, which he showed to be a true Foraminiferan and not a Zoophyte. He repeats Ehrenberg's feeding experiments, and demonstrates that the pigment is *not* passed into definite fixed stomachs, but becomes consolidated into small spherical masses which are circulated freely in the Sarcode until the digestible parts are removed, the residue being then rejected from the body. He shows that the contractile vacuole has nothing to do with reproduction, and regards it as a probable respiratory organ. He discovered the reticulate pseudopodia, and demonstrated how movement was effected by them, and he was the first to

observe that Foraminifera could move along the surface film of water by pseudopodial action. He discovered the flagellate cells of sponges, but did not see the collars, and holds that the sponge is nothing more than a colony of Infusoria. Finally, he introduced the term Rhizopoda, in which "family" the Foraminifera were included.

The important results which were announced by Dujardin, and the remarkable soundness of his work both in observation and theory, placed the study of the Protozoa in a position from which further advances might be expected to materialise at any time. Although the founders of the cell theory, which was promulgated in 1838-9, did not concern themselves with the Protozoa, the effect of the theory on the investigation of the microscopic fauna was immediate and striking. Attention being now focused on the importance of an accurate and detailed knowledge of the structure of cells, it was manifest that the organisms which the researches of Ehrenberg and others had made widely known could not fail to claim a share of the attention of the new race of histologists. Indeed, the modern type of Protozoologist begins to appear with the establishment of the cell theory, and from this time the stream of research becomes continuous, and begins rapidly to widen and deepen. Already in 1839 we find Meyen suggesting that the Protozoa are single cells which may be directly compared with a single plant cell, and in the same year Purkinje compared the structural basis of the actively dividing animal and plant cell, and gave to it the name of *Protoplasm*.

In 1839 Hake published the earliest recorded observations on a Coccidian. He describes and

figures the oöcysts of *Eimeria stiedæ* of the rabbit's liver, but failed to interpret them as of parasitic origin. Leeuwenhoek had previously seen the same bodies in 1674, but his observations were not published.

Martin Barry was the first, in 1843, to apply the cell theory to the Protozoa. In a paragraph headed "The Infusoria compared with Cells," he holds that *Monas* and similar Flagellates are single cells, and have a nucleus which corresponds with the cell nucleus of higher forms. They increase in number by division just as cells do, and the multicellular *Volvox* colony arises by the division of a single cell in much the same way as the embryo arises by the cleavage of the ovum. It was von Siebold, however, who, in a masterly treatise published in 1845, definitely formulated the doctrine of the unicellular nature of the Protozoa, and was the first to use that term in the modern sense. The central so-called glandular body, he points out, is an ordinary cell nucleus, and the body itself consists of the structureless simple substance called by Dujardin the Sarcode. His group Protozoa is divided into two classes—the Infusoria and Rhizopoda—these classes being comprised somewhat as they are now. His definition of the group is worth quoting. The Protozoa, he says, are "animals in which the various systems of organs cannot be distinguished, and whose irregular form and simple organisation are represented by a single cell."

So far the Infusoria and Rhizopoda have almost monopolised the attention of naturalists, but in 1845, and particularly in 1848, when Kölliker completed his elaborate memoir on the genus *Gregarina*, important contributions to our knowledge of the

Sporozoa were published. K  lliker maintains that these parasites are unicellular animals, and identifies the nucleus, which, however, had previously been seen by von Siebold in *Gregarina* in 1839. He describes division of the nucleus and a condition which he interprets as fission, but this was probably a case of association or syzygy. He gives reasons for suspecting that the pseudonavicell  , the formation of which he had investigated with a considerable degree of success, might represent one method of propagation of Gregarines, and almost immediately, in 1848, this was shown to be the case by Stein. It was much later, in 1899, that Siedlecki observed the complete life-cycle of a Gregarine, and showed for the first time that each of the encysted pair of sporonts divides into gametes, which then proceed to fuse in couples. Hence there is no direct union of the original individuals, but they are brought together indirectly through their products.

In 1849 the first am  eba to be found parasitic in man, the *Entam  eba gingivalis*, which occurs in the mouth, was recorded by Gros.

Stein's admirable work on the life-history of the Gregarine was followed in 1849 and 1854 by an error of corresponding magnitude. His attention had been attracted to the Acinetaria or Suctoria, which had been fully explored for the first time by Ehrenberg, who had described a number of species, and he was led to adopt the view that they were the embryonic stages of Vorticellids. This is the Acineta theory, which became almost as famous as the polygastric theory of Ehrenberg, and, it may be added, enjoyed as brief an existence. Stein made no attempt to trace the complete life-history of either form, but drew his conclusions from iso-

lated observations. He was influenced by the following considerations: (a) the frequent close association of Vorticellids and Suctoria; (b) the occurrence of stages which were interpreted as intermediate between Vorticellids and Suctoria; (c) the Vorticella-like ciliate embryos which were produced by some Suctoria; (d) the emission of Suctorian embryos by certain Vorticellids and other Ciliates, the former being interpreted as the embryos of the latter. The last point was the most baffling feature in the case, but it was soon demonstrated that the alleged Ciliate embryos were derived from Suctorian parasites. Stein distinguished twelve types of Suctoria, which he linked up with twelve Vorticellid species in much the same way as we associate the medusa of a Zoophyte with its corresponding hydroid.

The Acineta theory was soon attacked, and it was finally dispatched in 1856 by Lachmann, who was able to establish that the life-histories of the two groups were complete in themselves and quite independent of each other. The theory, though it had no foundation in reality, nevertheless served a useful purpose in stimulating the important enquiries which laid bare the facts of the matter.

LECTURE II

THE distinction between animals and plants, however striking it may be in the case of the higher forms, has always been a fruitful source of controversy whenever the simpler organisms were in question. The incidence of chlorophyll and cellulose are sufficient to isolate the average plant, and although cellulose occurs in the Dinoflagellata, and a substance very similar to it was found in the Tunicata in 1845 by Carl Schmidt, we may nevertheless exclude it from the list of animal products. The case of chlorophyll is different. Apart from those species which are claimed both by the zoologist and the botanist, chlorophyll occurs in forms the animal nature of which is indisputable, such as *Stentor*, fresh-water sponges, hydra, and certain Turbellaria and worms. In 1851 Cohn established that the colouring matter of many diverse green animals was not only identical, but due to chlorophyll granules similar to those of the green Algæ, and he drew the legitimate conclusion, though he did not establish it by experiment, that these green animals must liberate oxygen like plants. Chlorophyll and its derivatives may occur in animals as the colour basis of green or yellow corpuscles, such as the zoochlorellæ and zooxanthellæ of Protozoa, as diffused pigment in some species of *Vorticella*, or as a pigment in certain tissues of Arthropods and Mollusca. It has now been demonstrated in nearly all cases that the green and yellow corpuscles are intrusive Algal cells, and

that the diffuse pigment is derived from the food, but it is still possible, though decisive proof is wanting, that the chlorophyll of certain Protozoa may represent a true animal product. Gamble and Keeble point out that since chlorophyll and hæmoglobin have been shown to be closely allied substances any a priori difficulty in admitting this possibility is removed. In 1879, and subsequently, Geddes established that the chlorophyll of the green and yellow cells of Planarians and Radiolaria photosynthesises carbohydrate with the evolution of oxygen and the production of starch, and morphological evidence was produced in 1882-3 by Brandt, who showed that the yellow cells have a nucleus, a cellulose wall, a chromatophore with chlorophyll, a pyrenoid and starch inclusions, and, further, that they produce a biciliate swarm spore. The yellow cell therefore is a symbiotic plant, and is not an integral part of the Protozoan in which it is found. All this work, establishing as it does that chlorophyll is probably never an animal product, emphasises still further the fundamental divergence of animals and plants.

Our knowledge of the Radiolaria begins in 1834, when two species were described by Meyen. In 1851 Huxley published the first accurate observations on a living Radiolarian in his description of the new genus *Thalassicolla*, which he frequently observed during the voyage of the *Rattlesnake*. Huxley's genus included colonial as well as simple forms, and has since been split up into five genera. The genus *Thalassicolla*, as we know it now, is a non-colonial form without spicules, but Huxley properly assigns the species investigated by him to the Protozoa, and he describes the nucleus, central capsule, yellow

cells, and extra-capsular jelly. He regards the genus as "the connecting link between the sponges and the Foraminifera," the spicules being compared with those of sponges and the perforated central capsule with the Foraminiferan shell. A few years later, in 1858, after the ray-like pseudopodia of *Thalassicolla* had been observed, Johannes Müller correctly placed the genus and others similar to it among the Rhizopoda of von Siebold, and grouped the new forms together under the name of Radiolaria. It should be noted, however, that Müller's Radiolaria included the Heliozoa.

In 1852 Perty was the first to introduce the term Ciliata, and in the following year Cohn instituted the Flagellata, but it was only some years later that these groups were extended and properly defined by Claparède and Lachmann, who added another group—the Suctoria.

The first Flagellates to be found in the human body, apart from the *Lambliæ* discovered by Leeuwenhoek, were described from the excreta of cholera patients by Davaine in 1854. These he assigned to two varieties of the species "*Cercomonas hominis*," but Dobell and others have since identified them as a *Trichomonas* and a *Chilomastix*.

A few years afterwards two well-known general works on the Protozoa commence publication—the first by Claparède and Lachmann on the Infusoria and Rhizopoda, which was begun in 1858 and finished in 1861, and the second by von Stein on the Infusoria, the first part of which appeared in 1859 and the last in 1883. From the strictly observational point of view the work of Claparède and Lachmann is admirable, and many significant life-histories are carefully and for the most part accu-

ately described, but it is unfortunate that they should have opposed the unicellular interpretation of the Protozoa of von Siebold on grounds which led them to brigade the Protozoa rather with the Coelenterata and Annelida. This is nothing less than pure Ehrenbergism. Apart from the aberration which was responsible for the Acineta theory, which Claparède and Lachmann finally disposed of, Stein's monograph demands the fullest recognition. He aims at providing descriptions and figures of all known species of Infusoria, and his admirable arrangement of the Ciliates, based on the precise character of the ciliation, is still the foundation of our classification of the group. He abandons the Acineta theory almost completely, and regards the Infusoria as representing the highest type of Protozoa, but he is disposed to claim that their organisation is more complex than is admitted by Siebold's unicellular theory, the star-like phase of the contractile vacuole reminding him of the excretory system of Turbellaria and lower Annelids. He supports James-Clark in the view that the existence of the collared Flagellates is suggestive of an affinity with sponges, and he is the first author to recognise the close relationship of the Cysto- and Dinoflagellates.

In 1862 appeared the first noteworthy publication by Haeckel on the Protozoa, and his work is now sufficiently remote from contemporary prejudice to justify a candid examination of its merits. It begins and ends with elaborate researches on the Radiolaria published between 1862 and 1888, so that his working life as a Protozoologist covers about twenty-six years. Much of this work is classificatory. He institutes the Heliozoa and the Protista—a third kingdom intermediate between

animals and plants, in 1866, and the Cystoflagellata—now regarded as Dinoflagellates, and the Monera—undifferentiated organisms without nuclei, in 1868. In 1869 he separates the sponges from the Protozoa, and in 1873 he published his most famous systematic generalisation—the division of the animal kingdom into Protozoa and Metazoa, in doing which he definitely identifies himself with Siebold's view that the Protozoa are unicellular animals.

Paradoxical as it may seem, there is no doubt that Haeckel's scientific opinions were to a large extent perverted by the fact that he combined with a brilliant imagination a sincere conviction of the truth of evolution. As an evolutionist he believed in the origin of life from the simplest of beginnings, and in the existence of intermediate types by means of which the animal kingdom could be welded into one continuous whole, instead of being represented by a number of self-contained and unrelated groups. He made it one of the aims of his scientific life to discover these intermediate forms, and in this dubious quest he claims to have been largely successful. "Seek and ye shall find" is an admonition which, whatever its value in the world of ethics, is a double-edged weapon in the hands of a man of science. For the scientific investigator is often engaged in a quixotic search for the non-existent, and to succeed in such a task can only be attributed to powers of self-deception or invention which belong properly to the world of romance.

The famous *Gastræa* theory which was first enunciated by Haeckel in 1872, and subsequently developed in 1873, 1875, and 1876, is a characteristic expression of his theoretical bias. It assumes that living matter was first produced in the form of

amœboid blobs of jelly consisting of a homogeneous Sarcode without nuclei, which reproduced itself by simple fission. Such a type he claims actually to have found in the genus *Protamœba*. From this genus the transition is easy to another of his discoveries, *Protomyxa*, in which the phenomenon of segmentation appears, and with it the possibility of a metazoan animal. The next link in the series is *Magosphæra*, a "remarkable and instructive Protozoan," which he first studied, he tells us, in September 1869, off the coast of Norway, and the first description of which was published in 1871. It is instructive to note how closely this "permanent blastosphære" fits in with the scheme. It starts as a creeping amœba which, after a period of growth, loses its amœboid form, becomes rounded and encysts, and finally produces the mature multicellular ciliated "blastosphære" by a process similar to the segmentation of the egg. The mature stage now dissolves into its component ciliated cells, which proceed to revert to the amœboid phase with which we started. *Magosphæra*, *Protomyxa*, and *Protamœba* are thus permanent phylogenetic stages, which appear to have persisted since the dawn of the organic world, in order that we may be reminded how the earliest forms of animal life came into existence.

The crowning achievement of the Gastrœa theory, however, was the discovery of the permanent gastrula, without which the theory would have lacked that element of circumstantial corroboration which distinguishes, and at the same time betrays, the workmanship of the amateur creator. In 1862 Bowerbank described the "smallest known British sponge" under the name of *Haliphysema*, and a few

years later, in 1870, Carter, after a re-examination of the genus, correctly pronounced it to be not a sponge but a Rhizopod. Nevertheless, Haeckel in 1876 assigned a complex structure to *Haliphysema*, and held it to be a permanent gastrula and the archetype of sponges and Metazoa. He describes a body wall of two layers, and a large central cavity communicating with the exterior by a mouth. The body wall consists of an amorphous nucleated outer layer, and an organised inner layer or gastral lining formed mostly of flagellate collared cells, but including some very large nucleated cells interpreted as eggs. In the neighbourhood of the mouth there is a spiral series of particularly large flagellate collared cells which waft the food into the gastral cavity. In the allied genus *Gastrophysema* even gland cells and spermatozoa are found in the endoderm, and the central cavity is partially divided into two chambers, the lower one being associated with the germ cells, whilst the upper one is concerned solely with the function of nutrition. In 1878 Saville Kent published a complete denial of Haeckel's statements on the structure of *Haliphysema*, and justified his conviction that the animal should be classified with the Foraminifera, but the weighty authority of Haeckel's name, and the parade of detailed accuracy with which his description had been accompanied, operated in his favour, until the confirmation of Saville Kent's results by Lankester and others finally disposed of *Haliphysema* as a living gastræad. Haeckel himself, however, never admitted the charge of grave inaccuracy which had been brought against him. Years afterwards he was still publishing the old figures of *Haliphysema* in his general works, the name having

now been altered to *Prophysema*, in deference to his new contention that the animal he had originally described, though externally indistinguishable from the *Haliphysema* of Bowerbank and Saville Kent, was notwithstanding another genus known only to himself. "I must lay claim," he says, "to that liberty of natural philosophical speculation without which, in my opinion, general biology cannot advance a step forwards." Whatever differences of opinion may arise on this claim, we shall all agree that the obligation of the man of science to describe the facts as he finds them must be maintained against any "abuse of the privilege of fiction."

Haeckel's massive report on the *Challenger* Radiolaria, to which he devoted ten years of his life, was published in 1887. It was not confined to the *Challenger* material, but aimed at being a complete monograph of the group up to the time of publication, and to a large extent it may be said to fulfil this purpose. The species described number 4,318, of which 3,508 are new, and all previous literature is critically examined and its important findings incorporated in the text. There is a lengthy introduction of a general character, but the bulk of the work is concerned with systematics. In the atlas there are a number of delightful coloured figures drawn apparently from living examples, and some of the species in question were doubtless examined and sketched by Haeckel during his numerous travels from the living condition. Confining ourselves, however, to the *Challenger* collections, we find that, although they reached him in the form of spirit material and microscope slides stained with carmine, the same finished drawings, showing complete details as to living form and

colour, are frequently given. All who have examined Sir John Murray's slides of Radiolaria mounted during the voyage of the *Challenger* must admit that they are admirable and even beautiful preparations, but no one would claim that they justify the highly elaborate figures based on them by Haeckel. His infirmity, indeed, mixes with everything that he does, and we can only regret that, in publishing these figures, it was not frankly stated that they reflected the sublime visions of the author rather than the dull facts of nature.

In 1865 the flagellated organisms were grouped together by Diesing under the name of Mastigophora, and immediately afterwards, in 1866-7, James-Clark discovered an entirely new type of Flagellate, the collar-bearing monads, for the reception of which Saville Kent instituted the Choanoflagellata in 1880. At the same time James-Clark established the occurrence of collared cells in sponges, which led him to propound the view, previously suggested by Dujardin in 1838, that sponges had arisen as aggregations of flagellate Protozoa.

The first intestinal amoeba to be found in man was the harmless *Entamoeba coli*, described by Lewis in 1870, and in 1875 Lösch records the first pathogenic amoeba—*Entamoeba histolytica*.

The doctrine of spontaneous generation was a natural and obvious solution of a problem which otherwise threatened to become a permanent charge on the activities of biologists. Nevertheless, the controversy has existed in some form since the time of Aristotle, and cannot even now be regarded as extinct. From time to time it flares up and dies down, as protagonists of either side arise to challenge the verdict by the production of fresh evidence. It

is well known that the first important contribution on the experimental side was made in 1668 by Redi, who demonstrated that the larvæ which appear in decomposing flesh hatch out from eggs laid there by flies, and that if the flies were kept off by netting, the flesh putrified but did not become verminous. Redi, however, failed to carry this important discovery to its logical extreme, for he still continued to believe in heterogenesis, and argued that the larvæ which he found in plant galls were the progeny of the tissues of the plant itself. "I cannot refrain from saying," he adds, "that I do not consider it a great sin against philosophy to maintain that the worms of plants are created by the same natural principle that produces the fruits of the plants." Experiments which must rank almost equal in importance with Redi's, but which attracted much less attention, were published by Joblot in 1718. He was the first to sterilise with heat, and to show that Infusoria do not reappear in a hay infusion which has been boiled and isolated, but that if the infusion be then freely exposed to the atmosphere living forms are generated in it. He draws from his experiments the striking, but not altogether original, conclusion that the lower stratum of the atmosphere is filled with minute living animals, the gravitating germs or young of which account for the appearance of life in the unprotected hay infusion. He thus opposes spontaneous generation, and does so in language of remarkable emphasis. In 1765 and later, Spallanzani, as the result of a long and ingenious series of experiments, supported and developed the view that minute germs were constantly present in the atmosphere, and he held that these germs were

capable of developing when brought into contact with an appropriate medium. In this way only could the rapid multiplication and distribution of the smaller Infusoria be explained. Spallanzani also introduced an important modification of Joblot's procedure. The infusions were put into a flask, which was hermetically sealed and *then* boiled. Hence not only the infusion itself but the residual air in the flask could be effectively sterilised. In such an experiment no life appeared in the infusion however long it was kept, although this result was not without its exceptions.

The conflict was now in full swing, led by redoubtable champions on both sides. On the one hand Lamarck takes the view that the simplest organisms "are unable to leave behind them any permanent security for new generations," and hence that they are "as easily destroyed by environmental changes as brought into existence." Opposed to this we have the extreme position taken up by the Panspermists, such as Bonnet, who postulated that ubiquitous germs pervaded matter of all kinds, both organic and inorganic, and that some of them were so tenacious to life that they might almost be described as indestructible. On this understanding there were no limits to the environment in which living organisms might appear, and the occurrence of spontaneous generation was rendered unnecessary and even impossible.

It is obvious that nothing but a series of really crucial experiments could resolve an issue of so subtle a character. Even the germ theory of disease was implicated, since, if spontaneous generation occurred, the difficulty of abolishing zymotic disease might be insuperable. In 1859, 1860, and 1861,

the relevant papers of Pasteur were published, and the simple and direct methods by which he finally demonstrated the existence of a minute atmospheric fauna and flora, and its bearing on the appearance of organisms in organic infusions, so convinced his contemporaries that the belief in spontaneous generation was almost entirely abandoned. He collected these floating Infusorial germs, and cultivated them in sterilised media, but he showed also that over a glacier, in the clean atmosphere of the mountain top, and in the catacombs of Paris, appropriate media could be exposed without undergoing Infusorial contamination. In this respect he was unable to confirm the beliefs of the extreme panspermatists. In 1876, 1877 and 1878 Tyndall, by making use of an electric beam, showed not only how the presence of particles in the atmosphere could be detected, as Pasteur had done before him, but also how this method could be employed to establish the fact that organisms begin to reappear in a sterilised infusion within three days after atmospheric germs have had access to it. In fact, Tyndall may be described as having in a measure actually seen what Pasteur had only deduced. His brilliant and delightful experiments also cover such questions as the discontinuous distribution of atmospheric germs, and the methods of destroying them by heat. No candid mind can examine the evidence so magnificently marshalled by Pasteur and Tyndall without a feeling of sympathy for an opposition which had not only been routed but destroyed. Spontaneous generation, it is true, might still be an open question, but the foundations on which it had rested in the past could never be restored.

Between the researches of Pasteur and Tyndall,

in 1870 and 1874, Bastian published his works on the origin of life. He considers that *Amæba* is too simple an organism to have had a lengthy phylogenetic history, in which case the synthesis of living matter must still be proceeding. In supporting the doctrine of heterogenesis he relies on two main lines of argument. "Well-informed men of science," he says, "no longer doubt that swarms of Bacteria can be made to appear within sealed glass vessels containing suitable fluids, after the vessels and their contents have been exposed to the temperature of boiling water. The thorough establishment of this fact has been of the greatest importance." "The question of 'spontaneous generation,' therefore, stands in this position. If it be really true that all known forms of living matter are killed by a brief exposure in the moist state to the temperature of 212° F. there is no longer room for doubt. The occurrence of 'spontaneous generation' must in this case be admitted as an established fact, or 'Law of Nature.'" Bastian's second point, a purely negative one, is that the particles in the air had never been proved to be derived from, or to develop into, the alleged parental infusion organisms. The fallacy of his first contention was exposed by Tyndall, who, by applying a method somewhat analogous to the fractional distillation of the chemist, succeeded finally in destroying the most refractory germs, and in producing a permanently sterile infusion. The second point we may now consider.

It must be clear that Pasteur and Tyndall, though they succeeded in re-establishing the *status quo*, exploited the physical aspect only of the issue, and by doing so proved not only that the case for spon-

taneous generation had not been demonstrated, but that the facts were not inconsistent with the known sequence of normal generation. They were, however, not Protozoologists, and had no evidence to offer in respect of the habits and life-histories of infusion organisms. Nevertheless, the convincing testimony of microscopic observation is indispensable in all enquiries of this character. To complete the case, therefore, a laborious research of considerable difficulty and refinement had to be undertaken, but the highest honours awaited the investigator who would faithfully accomplish this difficult task. It was attempted by Dallinger and Drysdale, and they claimed to have produced the missing evidence in their publications of 1873, 1874, and 1875. Their methods were heroic. They attempted to keep a single Monad under continuous observation, day and night, using the highest powers of the microscope, in the hope that its complete life-history would be disclosed. Whether this is possible, owing to the rapid movements of the species studied and the necessity of occasionally changing the lens of the microscope, has been doubted, but it was at least seriously attempted. The tedium of this ceaseless vigil was relieved by the lively expectation that events of importance might supervene at any moment. In 1878 Dallinger himself published an account of the life-history of a "minute septic organism" which was afterwards named by Saville Kent *Dallingeria drysdali*. This is one of the tri-flagellate forms having a maximum length of $\frac{1}{4000}$ th of an inch, and, according to Dallinger, after a period of longitudinal fission, two individuals come together, lose their flagella, fuse both as regards their bodies and their nuclei, and encyst. A period of

spore formation of from three to five hours follows, at the end of which the cyst ruptures and liberates a cloud of "exquisitely minute specks" which only become visible, even under a magnification of 5,000 diameters, when the conditions for observation are most favourable. These spores then proceed to grow and develop flagella, and at the end of four hours have attained the adult form but only half the adult size. By the end of the fifth hour the mature size is reached, and fission is resumed very soon afterwards. Dallinger and Drysdale allege that the adult forms are "utterly destroyed" by a temperature of 150° F., but that the spores can sustain a fluid heat of 220° F. and a dry heat of from 250° to 300° F.

The point of fundamental importance which Dallinger and Drysdale claim to have established is the existence of ultra-microscopic spores which can withstand very high temperatures. If they are right in this, Bastian's results are at once explicable, since the only consequence of a single boiling is to destroy all *apparent* signs of life, the reappearance of organisms in the supposed sterile infusion being due to the development of the undestroyed and almost invisible spores. Unfortunately, however, no subsequent observer has succeeded in confirming the existence of the ultra-microscopic spores of Monads, and it seems certain that Dallinger and Drysdale misinterpreted what they saw, and describe, not a significant phenomenon of life and procreation, but the onset of death, and the dissolution of the organism into the earth from which it sprang.

The first general treatise on the Protozoa of the American continent was the *Fresh-water Rhizopods of North America*, by Leidy, published in 1879.

According to H. F. Osborn, Leidy "never made an incorrect observation or published an incorrect figure." His work is concerned largely with the Lobosa, of which group it forms a beautiful systematic monograph. The field, however, had been too exhaustively explored by Ehrenberg, Dujardin, and others to yield many novel forms, and the chief interest of Leidy's work is represented by its important bearings on the distribution of the fresh-water Protozoa.

In 1880 Munier-Chalmas suggested the existence of dimorphism in the fossil Foraminifera, and the two forms were afterwards named megasphere and microsphere. In 1895 J. J. Lister established this discovery by showing that it was not a case of sexual dimorphism, but that the two forms were "members of a recurring cycle of generations," or, in other words, that the principle of alternation of generations was exemplified in the Protozoa.

The bearing of systematic work is so important, especially in researches concerned with complex life-histories, that I must not omit reference to certain contributions towards the modern classification of the Protozoa which were made at about this time. In 1879 Leuckart instituted the Sporozoa, to include the Gregarines and the Coccidians, and in 1880 Bütschli set up the comprehensive group which he named Sarkodina. This term, however, had previously been used, but in a different sense, by Hertwig and Lesser in 1874. Bütschli is also responsible for the institution of the Myxosporidia in 1881, and the Dinoflagellata in 1885. Balbiani established the Sarcosporidia in 1882, but the inclusion of *Sarcocystis* among the Protozoa has recently been questioned. The Hæmosporidia were

first considered to be a distinct group by Danilewsky in 1885 and 1886, but he named it Hæmocytozoa, and his conception of the group is not in strict accord with modern usage. Doflein (1901) was among the first to use the term in the modern sense, and to give a satisfactory definition of it. According to Dobell and other recent workers the order should be dissolved and its members classified as blood-inhabiting Coccidia.

In 1888 and 1889 Maupas published his researches on the conjugation of the Infusoria, and it is not too much to say that this work will ever remain one of the most significant achievements in the whole range of zoological literature. I say this not so much on account of the specific discoveries which he made, important as they are, but because he succeeded in diverting research to the cytological aspects of the generative process. In this work, however, he was not without predecessors. In 1858 and in later papers Balbiani had described conjugation in *Paramecium*, and had regarded it, not as the result of longitudinal fission, as was the practice at the time, but as an act of sexual union, resulting in reciprocal fertilisation of the hermaphrodite conjugants. He had even seen the mitotic figure of the micronucleus, but had misinterpreted the spindle as a bundle of spermatozoa, whilst the meganucleus was considered to be the ovary. This theory of the sexuality of the Ciliates is contemptuously referred to by Maupas as "a discovery sufficiently feeble." Engelmann in 1875 successfully attacked the sexual theory of Balbiani and Stein, and asserted that the continued fission of Ciliates resulted in degeneration, conjugation being, not a method of reproduction, but a process of nuclear reorganisation.



ÉMILE FRANÇOIS MAUPAS (1842-1916)
From a medallion struck in 1913

In 1875-6 Bütschli published works only less important than those of Maupas himself, which indeed they had directly inspired. He establishes the true nature of the micronucleus by showing that it divides mitotically like an ordinary cell nucleus. He traces the fragmentation and disappearance of the meganucleus, and thus proves that the nuclei of the ex-conjugants are derived from the micronuclei only of the conjugants, and not from the fragments of the meganucleus. He agrees with Engelmann that the function of conjugation is to effect rejuvenescence, and the ensuing renewal of fission is to be compared with the formation of the multicellular metazoan body. "The theory of Bütschli," says Maupas, "represents an immense advance on previous work, and places the study of the fertilization of Ciliates on a solid foundation, free from all those false hypotheses and arbitrary interpretations which had previously encumbered it."

The view that the object of conjugation is to reanimate an otherwise decadent and senile stock, and so restore the powers of growth and fission, was held by several observers before Maupas, but Maupas claims to have established it by piecing together the history of various species so as to display the entire life-cycle in each case. Periods of growth and asexual fission are said to alternate with periods of quasi-sexual conjugation. If for any reason conjugation does not occur, a third or senile period is entered upon, in which the individuals undergo physical degeneration, and at the end of which death supervenes. The length of these periods is fixed for the species, but varies in different species. Conjugation, therefore, is an act of rejuvenescence,

failing which the stock becomes extinct. The highly significant and complex nuclear manœuvres which accompany conjugation are described in detail, and have been substantially confirmed by later observers. Only those who have endeavoured to check these results will understand how much lies behind his simple reference to the "long hours of labour which the work had cost him." Maupas also studied the factors which control rate of fission, and it is interesting to note that he recognised the importance of the character and abundance of the food supply. Another point which attracted his attention was the effect of in-breeding, and he favoured the conclusion that conjugation between genetically related forms either did not occur at all or was abortive when it did. In other words, senescence and death awaited all individuals which had not opportunities for conjugation with unrelated stocks.

Subsequent research has failed to confirm Maupas' results in two important respects. Conjugation between related forms occurs normally, and is not necessarily abortive, nor is conjugation and nuclear reorganisation indispensable to the continuance of the stock. It was in 1881 that Weismann, by his dramatic announcement that the Protozoa were immortal, drew the attention of the public to an obscure and neglected corner of the animal kingdom. The first announcement of this novel phenomenon, however, came from "the Attic lips of S.T.C." In October 1815 Coleridge the poet had completed his *Biographia Literaria*, which was subsequently published in July 1817, and in this work appears the following interesting passage: "There is a sort of *minim immortal* among the animalcula infusoria

which has not naturally either birth, or death, absolute beginning, or absolute end: for at a certain period a small point appears on its back, which deepens and lengthens till the creature divides into two, and the same process recommences in each of the halves now become integral." Ehrenberg in 1838 was the first naturalist to discuss this view, but his opinions are less clearly expressed than those of Coleridge. He says: "It is as though one were to divide oneself into innumerable new parts in order to live for ever and to remain young." Following the less complete statements of Balbiani in 1860, Maupas was the first to traverse the doctrine of Protozoan immortality, and to support his statements by the production of detailed evidence. If conjugation, he says in effect, is an essential factor, and the life of these animals must in consequence follow a definite undeviating cycle, it is obvious that death, even if it does not take the form of a natural recurrent phenomenon, is nevertheless a possibility which must sooner or later be faced.

On February 1, 1901, Calkins started the culture of two different lines of *Paramecium caudatum* with the object of testing experimentally whether conjugation was a vital factor in the life of this species. He argued that if Loeb "could induce artificial fertilization in the echinoderm egg, it should be possible to induce artificial rejuvenescence in *Paramecium*." By a modification of Maupas' methods of isolation it was possible to inhibit conjugation and to substitute for it an artificial stimulus. Accordingly, when his stocks, after periods of fission, began to weaken and die, he changed the diet or applied some chemical stimulant. He used vegetable and meat infusions such as the clear extract of lean

beef, extract of brain and pancreas, and also salts of sodium, magnesium, and potassium. The result was that, although the usual life-cycle of *Paramecium* in culture is from 150 to 170 generations, one of Calkins' lines survived to the 570th generation, and the other, covering a period of 23 months, to the 742nd. This experience, showing as it did that death could be postponed and rejuvenescence effected without the aid of conjugation, modified Maupas' conclusion but did not actually disprove it. The refutation, however, was to come. On May 1, 1907, Woodruff initiated a culture of *Paramecium*, in which the possibility of conjugation was absolutely precluded, which is still proceeding, and up to the summer of 1924 had produced some 11,000 generations. There seems no reason, provided the appropriate conditions are maintained, why it should not go on for ever, and we must therefore admit that the potential immortality of the Protozoa has at length been definitely established.

The Protozoan parasites of the blood have only been made the subject of an intensive study since their association with important diseases of animals and man was established. When we survey the piles of literature on blood parasites which exist at the present moment, it is difficult to realise that many of us, against whom the charge of old age can scarcely be levelled, are yet old enough to remember the time when these parasites were unknown to the working zoologist. The big textbooks on the Protozoa published in the eighties and nineties by Bütschli and Delage and Hérouard include only casual references to the trypanosomes and no mention of the organisms of malaria. A great propor-

tion of this work, therefore, is too recent to be made the subject of an historical enquiry, and I only propose to deal very briefly with the preliminary investigations, of which, however, the vast developments of modern times are the direct outcome.

The first mention of the disease known as sleeping sickness appears in a publication by Atkins in 1734, but it was not until 1841 that a "trypanosome" was discovered, Valentin finding the Flagellate (? *Trypanoplasma*) in the blood of the salmon. Almost at once, in 1842 and 1843, Gluge and Gruby discovered trypanosomes in the blood of the frog, for which the latter author instituted the genus *Trypanosoma*. In 1878 Lewis describes a trypanosome in a mammal—the *T. lewisi* of the Rat; and two years later, in 1880, the first suggestion that a trypanosome was the cause of disease was made by Evans, who found *T. evansi* in the blood of horses suffering from Surra. Detailed comparative studies of trypanosomes were carried out by Mitrophanow in 1883-4, and by Danilewsky in 1885, '89. The association of the parasites with disease was again emphasised in 1895, when Bruce discovered a trypanosome in the blood of horses and cattle suffering from tsetse-fly disease in South Africa, and in the following year he demonstrated, both by observation and experiment, the rôle of the tsetse-fly as a carrier of the disease. He was therefore the first to discover that a Protozoal disease could be transmitted by an insect. In 1878 Manson had already established the necessary intermediation of an insect in the development of the filarial parasite, and in 1893 Smith and Kilborne had shown that the *Piroplasma* of Texas cattle fever was transmitted by ticks, but Bruce's important discovery

had the still more important and far-reaching result of focusing attention on the part played by *Insects* in the dissemination of *Protozoal* disease. Bruce, however, did not regard the fly as the alternate host of the trypanosome, but believed that it was responsible only for the mechanical transmission of the parasite.

So far the human Flagellates had been neglected, and it was not until 1898 that Nepveu described a "trypanosome" in the human blood. The identification in this case, however, is doubtful, and Dutton's *T. gambiense* of 1902 is the first unassailable record of a human trypanosome. Later still, in 1903, Castellani first "suggested as a working hypothesis" that a trypanosome in the cerebrospinal fluid was the cause of sleeping sickness in man. In one respect there is an interesting parallel between the history of sleeping sickness and that of malaria, since in both cases the life-history of the parasite was first established in an animal species, and the knowledge so gained afterwards applied to detect the cause of a human disease.

There are few events in the history of Zoology more fascinating and instructive than the history of our knowledge of the organisms of malaria. Now that the main facts have been repeatedly confirmed, and have lost the charm of novelty, the difficulties which confronted the medical officers who were grappling with the problem on the spot, under climatic conditions which taxed their health and energy to the utmost, are either forgotten or ignored. The importance of a laboratory training in Parasitology, and, we may add, in systematic Zoology also, is apparent in almost every page of the narrative which Ross has recently published of his

early struggles with the problem. "I went forth," he says, "very badly equipped for the fray," and how much valuable time was wasted, and how near he came to failure owing to his lack of acquaintance with the methods and literature of Protozoology and the classification of mosquitoes, is an impressive testimony to an enthusiasm which could succeed under so grave a handicap.

One of the earliest observers to hint at a relationship between gnats and malarial fever was Lancisi, who, as early as 1717, worked out the life-history of the mosquito, and had vague suspicions that it was in some manner responsible for the disease. Nothing further of importance was done until November 6, 1880, when Laveran observed the malarial parasite in the human blood, and published a description of it in the following year under the name of *Oscillaria malaricæ*. He saw the amœboid, rosette, sphere, crescent, and flagellate stages, and "from the first divined that the mosquito is connected with the propagation of these parasites" (Ross), but he did not determine the relationships of the stages he had discovered, nor did he recognise their animal nature. In 1885 the genus *Plasmodium* was instituted by Marchiafava and Celli. In 1886 and 1889 Golgi described the division of the amœboid form into merozoites, he showed that the simultaneous liberation of these spores coincided with an attack of fever in the patient, and that the quartan and tertian fevers were produced by two distinct species. The first demonstration that the parasite was not a plant, but probably one of the Protozoa, was made by Metchnikoff in 1887, and in 1891 Danilewsky described in greater detail the flagellate stage previously seen by Laveran. He

regarded it as a separate flagellate parasite, and instituted the genus *Polymitus* for its reception. This interpretation was soon questioned, and in 1894 and 1896 Manson suggested that the *Polymitus* was a flagellated spore stage of the parasite, which passed into the stomach of a blood-sucking mosquito or "a similar suctorial insect," and from thence found its way into drinking water. The significant fact observed by Manson was that the *Polymitus* stage was not found in the human body, but only developed *after the blood was drawn*, which led him to suspect that the natural host of this stage must be a blood-sucking insect. Of Manson's share in the discovery Ross remarks: "His brilliant induction so accurately indicated the true line of research that it has been my part merely to follow its direction." A very important advance was now made by MacCallum in 1897-8. Working with the "*Halteridium*" and *Plasmodium* cycles, he showed that the so-called *Polymitus* consisted of microgametes or spermatozoa which became detached and fertilised the female crescents to form zygotes.

By this time the solution of the problem was in the air, and might be precipitated at any moment. It fell to Ross to apply the requisite stimulus. On May 21 and October 11, 1898, appeared his well-known Reports on the Cultivation of *Proteosoma* in Grey Mosquitoes and in Birds, in which he established that the parasites were extracted from the blood of malarious sparrows, and introduced into the blood of healthy individuals, by a blood-sucking fly. The fly in question was *Culex fatigans*, but it was not identified by Ross. The stages through which the parasite passed in the body of the fly were recognised and demonstrated, and *both* hosts were shown

to be essential to the complete life cycle of the parasite. The fly therefore was not a mechanical carrier but an obligate host. The point in these Reports which was entirely novel and of the first importance was the demonstration that the sporozoites travel forwards in the body of the mosquito into the salivary glands, and are therefore injected with the salivary secretion into the blood of the vertebrate host when the fly is feeding. To sum up, the foundation of our knowledge of the schizogonous cycle of the malarial parasites in their vertebrate hosts is the work of Golgi (for the human parasites), and of the sporogonous cycle in a blood-sucking fly the work of Ross (for the parasites of avian malaria).

Since the publication of the Reports on *Proteosoma* a prolonged and embittered controversy has done much to rob the malaria problem of its attractive setting. Into that controversy it would be unwise to enter, but one observation may perhaps be permitted. If the study of the history of science emphasises one point more than another, it is that the research of greatest significance is that which leads us from the beaten track into an unoccupied and fertile country. The labourers who follow in the wake of the pioneer may be trusted to exploit what they could not have discovered. It is impossible to doubt where the merit lies in such a case, and it is equally difficult to question that the ultimate solution of the subtle problem of malaria in man was indicated in the *Proteosoma* Reports of Ross.

The history of the Coccidian parasites begins with their discovery by Hake in 1839, but the first important observations on a Coccidian were published in 1855 by Kloss, who discovered the organism now

known as *Klossia helicina* in the renal organ of *Helix*. In 1870 Eimer described parasites of the gut and liver of various animals, including man, which have since been included under the genera *Eimeria* and *Isospora*, and in 1892 an important work by Pfeiffer was published, which contained the theory of alternate generations, and foreshadowed the comparable development of the malaria parasite in the mosquito. In 1897 Schaudinn and Siedlecki show that the macro- and microgametes of *Coccidium* conjugate to form zygotes—thus anticipating the analogous advance in our knowledge of the malaria cycle. In 1898, the year in which the latter cycle was pieced together by Ross, Siedlecki published an account of the sexual cycle of the Coccidian *Aggregata* (“*Klossia*”), which is now known to be parasitic in two different hosts, a cuttle-fish and a crab, and exhibits a regular alternation of generations. “In this work Siedlecki described correctly, for the first time, the whole sexual cycle and sporogony of *A. eberthi* in *Sepia*: he described the development of the microgametes and macrogametes, and the process of fertilisation: and on the basis of his observations he correctly referred the organism to the Coccidia. . . . It is a work of such general excellence that it constitutes one of the classics of Protozoology” (Dobell). In 1899 Siedlecki gave also a detailed and admirable account of the entire life-history of *Adelea*. These researches, therefore, lead us easily and directly to another classic—the description of *Coccidium schubergi* published by Schaudinn in 1900, which must be regarded as the first adequate description of the *complete* life cycle of a Coccidian. In this work it is only just to point out that Schaudinn had received material assistance

from Siedlecki. The quality of Schaudinn's work on the Protozoa varies very greatly. Some of it is gravely inaccurate and speculative to a degree, but his *Coccidium* memoir is a masterpiece of sound observation and legitimate inference, and his reputation may well rest on this work alone. There is no occasion to discuss further a piece of research with which all students of Zoology become familiar in their first year of study.

In this brief analysis of the doings of Protozoologists I have attempted to illustrate not only the importance of success but the significance of failure. In criticising our predecessors we must not forget that we stand on their shoulders, and that we owe as much to their errors as to their wisdom. The ambition to detect and to correct error has played a large part in the history of science. The learned world is indeed a censorious and a suspicious world. One of George Eliot's characters is made to express this attitude in the following amusing passage: "I myself," he says, "for having shown error in a single preposition, had an invective written against me wherein I was taxed with treachery, fraud, indecency, and even hideous crimes. Such, my young friend—such are the flowers with which the glorious path of scholarship is strewed." All this striving and controversy, however, only serves to invigorate that regard for faithful observation on which all serious research must in the last resort depend. The secrets of this inscrutable Cosmos yield themselves only to the few. The work is difficult, mistakes are inevitable, and progress slow. Let us therefore preserve the memory of those who have emerged from this unequal contest if only with the humblest spoils of victory.

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